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Modeling the transport of larval yellow perch in Lake Michigan

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Abstract

The transport of larval yellow perch (*Perca flavescens*) in Lake Michigan is studied with a 3D particle trajectory model. The model uses 3D currents generated by the Great Lakes version of the Princeton Ocean Model driven by observed momentum and heat fluxes in June-August 1998, 1999 and 2000. Virtual larvae were released in the nearshore region with the most abundant preferred substrate for yellow perch spawning, rocks. We also investigated the potential for physical transport mechanisms to affect recruitment of Lake Michigan yellow perch by coupling hydrodynamic models with individual-based particle models of fish larvae to study variation in larval distributions, growth rates, and potential recruitment. Larval growth rates were simulated using a bioenergetics growth model with fixed consumption rates. Results indicate that lake circulation patterns are critical for understanding interannual variability in Great Lakes fish recruitment.

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Introduction

Yellow perch (*Perca flavescens*) is ecologically and economically important species in Lake Michigan that has suffered recruitment failures over the last decade (Francis et al., 1996). Causes for poor recruitment are not understood, but are believed to be a result of high mortality during the larval stage. Yellow perch have an early life history similar to many marine coastal species, which is a pelagic larval stage that is susceptive to physical transport. In inland lakes the pelagic stage, begins shortly after larvae hatch and lasts for approximately 40 days (Whiteside et al., 1985). In Lake Michigan the length of the pelagic period may be even longer, and at least some individuals can be captured in the pelagia after about 75 days. This extended pelagic period means the influence of lake physics on recruitment of yellow perch could be significant due to complex lake-wide circulation patterns.

The importance of meso-scale oceanographic features to fish population structure and recruitment variability has long been recognized for marine fish populations (e.g., Hjort, 1914). However, it has only been in more recent years that hydrodynamic models have been used to understand the impacts of marine physics on the recruitment. For example, Werner et al. (1996) used a 3-D hydrodynamics model, turbulence model, and models of foraging and growth to demonstrate the complementary interactions between circulation, trophodynamic processes and recruitment of cod *Gadua morhua* and haddock *Melanogrammus aeglefinus* on Georges Bank. Heath and Gallego (1998) coupled a particle-tracking model with an individual-based model of larval growth and survival to investigate the spatial and temporal patterns in recruitment processes of North Sea haddock *Melanogrammus aeglefinus*. In yet another study, hydrodynamic models were used to explain transport mechanisms for fish larvae recruiting from offshore to coastal estuaries in the South Atlantic Bight (Crowder and Werner, 1999).

Most studies quantifying the impact of physics on fish recruitment have been in estuarine and marine, with few in freshwater ecosystems. The Great Lakes, the largest freshwater system in the world, are frequently called inland seas because they experience similar physical processes as observed in marine systems. These physical processes occur over various temporal and spatial scales, and are very complex due principally to the wind driven forcing that generates these currents. Given the complexity and magnitude of the physical processes in Lake Michigan, it is very likely that these physical processes may play an important role in structuring the recruitment dynamics of Lake Michigan fishes. The goal of this paper is to begin exploring the effects of physical factors on recruitment variability of important Lake Michigan fishes in order to gain insight into the decline in the yellow perch populations and factors causing poor recruitment. The Great Lakes hold an important advantage over the coastal ocean because dispersal of fish larvae is relatively confined in the Great Lakes compared to dispersal in wide-open marine ecosystems like Georges Bank, the south Atlantic Bight or the North Sea.

In this paper, we apply a model-based Langrangian approach that utilizes 3-D circulation and thermal processes, physiology and ecology of fish larvae, and trophodynamics for understanding recruitment dynamics in Lake Michigan specifically, and the other Great Lakes in general. In the initial set of numerical experiments we focus on the transport of larval yellow perch hatched in the area in southern Lake Michigan known for high concentrations of rocky habitat preferred by yellow perch spawners (Figure 1). We couple models of circulation and temperature, with individual-based particle models of fish larvae to study variation in larval distributions, growth and survival rates, and potential recruitment.

Models

Hydrodynamic model

A 3-dimensional circulation model of Lake Michigan (Beletsky and Schwab, 2001) is used to calculate lake circulation. The model is based on the Princeton Ocean Model (Blumberg and Mellor, 1987) and is a nonlinear, hydrostatic, fully three-dimensional, primitive equation, finite difference model. The model uses time-dependent wind stress and heat flux forcing at the surface, free-slip lateral boundary conditions, and quadratic bottom friction. The drag coefficient in the bottom friction formulation is spatially variable. It is calculated based on the assumption of a logarithmic bottom boundary layer using constant bottom roughness of 0.1 cm. Horizontal diffusion is calculated with a Smagorinsky eddy parametrization (with a multiplier of 0.1) to give a greater mixing coefficient near strong horizontal gradients. The Princeton Ocean Model employs a terrain following vertical coordinate system (sigma-coordinate). The equations are written in flux form, and the finite differencing is done on an Arakawa-C grid using a control volume formalism. The finite differencing scheme is second order and centered in space and time (leapfrog). The model includes the Mellor and Yamada (1982) level 2.5 turbulence closure parameterization. The hydrodynamic model of Lake Michigan has 20 vertical levels with finer spacing near the surface and the bottom and a uniform horizontal grid size of 2 km (Figure 1).

Particle trajectory model

The 3-d particle trajectory code is a combination of the Princeton Ocean Model subroutine TRACE written by Jarle Berntsen (Institute of Marine Research, Bergen-Nordnes, Norway) and the second order accurate horizontal trajectory code described by Bennett and Clites (1987). The horizontal currents are first interpolated from velocity points to grid square corners on the Arakawa-C grid. By assuming bilinear variation of the horizontal currents within a grid square, the Taylor series expansion of velocities about the particle position in the trajectory equations yields a pair of simultaneous equations for the new particle position. The time step is chosen to limit the maximum excursion of a particle to 1/8 the distance between horizontal grid points. Vertical velocity is interpolated to z-coordinates from sigma coordinates based on bilinear interpolation of the depth to the particle position within a grid box. Particles are prevented from crossing the lake bottom or free snrface, as well as horizontal houndaries. This method generally predicts more realistic trajectories than traditional first-order horizontal methods and does not allow particles to accumulate in 'stagnation' zones at grid square corners along the shoreline.

Biological model

We grow larval yellow perch in the model by using a bioenergetics growth model. The bioenergetics model is a species-specific, energy-balance approach that describes the flow of energy through an individual fish and how that energy is partitioned among consumption, growth (somatic and reproductive), and losses (respiration, egestion, excretion, and specific dynamic action). Energy per unit time is related to weight per unit time by a specific energy density for predator and prey (calories per unit weight). The basic form of the bioenergetics model in terms of weight specific growth rate ($g \cdot g \cdot d^{-1}$) is,

$$\frac{1}{W}\frac{dW}{dt} = \phi - (R_{resp} + SDA + F + U)$$

where W is weight of the individual predator, t is time in days, ϕ is feeding rate, R_{resp} is respiration, SDA is specific dynamic action, F is egestion, and U is excretion. Each of the terms in the equation is a function of water temperature, thus both feeding rate ϕ and temperature drive growth. Parameter values were adapted from a previously published bioenergetics model for yellow perch (Rose et al.1999). For this exercise, we assume that ϕ is constant and growth rate is driven primarily by temperature, which differs across space and time.

Results

Physics

Hydrodynamic model run begins on January 1, 1998 and ends on December 31, 2000. Initial currents are set to zero. In the beginning of model run the lake is thermally homogeneous vertically, but there are small horizontal temperature gradients with warmest temperatures located offshore and coldest temperatures nearshore. Based on available observations, the model was initialized with water temperatures in the 2-4.5^{o} C range. Hourly meteorological data (wind speed and direction, air temperature, dew point and cloud cover) for 1998-2000 were obtained from 18 National Weather Service stations around Lake Michigan and National Data Buoy Center (NDBC) buoys 45002 and 45007 (Figure 1). These observations form the basis for generating

gridded meteorological fields. Details of heat and momentum flux calculations are presented in Beletsky and Schwab (2001), and details of a new spatial interpolation technique for meteorological data used in 1998-2000 simulations are presented in Beletsky et al. (2003).

Because temperature plays a crucial role in larval growth we present here monthly average snrface temperature patterns for each summer in 1998-2000 (Figure 2). There is a general north-south temperature gradient seen in all months in all years. Another prominent feature of lake temperature patterns is a wind-driven npwelling at the west coast typical of summer conditions in Lake Michigan (Beletsky and Schwab, 2001). In sonthern Lake Michigan, surface temperature steadily increased from about 17 °C in June to 22 °C in July to 23 °C in August of both 1998 and 1999. In all summer months of 2000 lake surface temperature was about 1-2 °C lower which should have important implications on larval growth as will be shown in the next section.

Lake circulation patterns can also play an important role in larval transport and survival. The characteristic short-term circulation pattern in a lake, which is driven by a spatially uniform wind, consists of two counter-rotating gyres; a counterclockwise-rotating (cyclonic) gyre to the right of the wind and a clockwise-rotating (anticyclonic) gyre to the left (Bennett, 1974). The strongest currents are downwind in the coastal regions while weaker upwind return currents develop in the deeper waters. This simple pattern is sometimes seen in monthly mean circulation patterns in winter, but in summer buoyancy effects make circulation more complex. Thus in southern Lake Michigan for most months, the circulation pattern consisted of two gyres with the cyclonic gyre confined to the deep area and the anticyclonic gyre in the shallow southernmost area (Figure 3). This circulation pattern was seen in previous simulations (Beletsky and Schwab, 2001), however, it is difficult to detemine if this pattern is typical due to the scarcity of long-term current observations in Lake Michigan (Beletsky et al., 1999). If an anticyclonic gyre is persistent in summer in southern Lake Michigan, it can trap yellow perch larvae in that part of the lake. During some months (August 1998, June and August 2000), a strong northward current from southern Lake Michigan penetrated the northern basin with significant implications for larval transport. The speed of mean surface currents varied from 10 to 20 cm/s.

In the particle trajectory model, 246 particles were released north of Chicago (Figure 1) at bathymetric depths of less than 10 m. This reflects the fact that yellow perch prefer to spawn on the rocky habitat available at this location. Particles were distributed uniformly with depth: near the surface, at 1/3 and at 2/3 of a grid cell's depth. Particle model runs began on June first of each year (1998, 1999, and 2000) and ended in the end of August. Particle locations at the end of each month are shown in Figure 4. Because all particles were released in very shallow waters they have a tendency to stay relatively close to the surface (0-20 m). There was no significant difference in movement of particles released near the surface and ones that were released closer to the bottom. Thus, we focused on surface currents and not depth-averaged currents. Overall, particle movement matches the monthly mean surface current pattern rather well: particles initially move offshore and then continue to circulate in southern Lake Michigan in an anticyclonic fashion. Under certain conditions (like a case of a particularly strong northward coastal current in August 1998) a significant number of particles escape the southern basin and penetrate the northern basin of Lake Michigan. The proximity of particles to shore at the end of the model run in August can also be critical for larval survival. Larvae about this time begin to metamorphose into their adult characteristics and move into adult habitat, which is near bottom and near shore. As model results show, in 1998 the number of particles reaching nearshore waters in August was significantly higher than in 1999 and 2000 which may provide a significant advantage for surival.

Biology

Biological model runs also began in June of each year. The hydrodynamic model supplies information on the three-dimensional temperature field along the larval path predicted by the particle trajectory model. Another critical parameter for larval development is food availability (primarily zooplankton). Unfortunately, there is very little information available on the spatial distribution of zooplankton in south Lake Michigan in summer. Therefore, in all biological model runs we assumed that there is no spatial gradient in food (zooplankton) available for larval yellow perch.

All larvae were assumed to have initial length of 6 mm at hatching. Movement and growth of larvae in the model were followed from hatching to 30 mm, the length at which they settle and become demersal; larvae metamorphose into juveniles at 20 mm, and by 30 mm take on the characteristics of adult fish. Growth rates and time to settlement were predicted assuming two different food availability scenarios. This was done by multiplying maximum consumption by 1.0 (Scenario 1) and 0.5 (Scenario 2). Locations of larvae which reached 30 mm length under the maximum consumption conditions (Scenario 1) are shown in Figure 5. No larvae reached 30 mm before the end of the first month except a small number in 1999. On the contrary, all larvae reached 30 mm by the end of the second month and therefore July and August locations match exactly those of Figure 4. In case of the reduced consumption scenario 2 (more typical of realistic Lake Michigan conditions) the situation changes dramatically. As expected, no larvae reached 30 mm by the end of June but by the end of July only a few larvae reached 30 mm in 2000 while in 1998 and 1999 more than 60 % of larvae grew to their settlement length (Figure 6). This is undoubtedly the result of much cooler water temperatures in 2000 predicted by the hydrodynamic model and confirmed by surface temperature observations at the NDBC buoy 45007.

Discussion and conclusions

This is the first physical-biological model of larval fish developed for the Great Lakes. The model shows significant interannual variability in particle transport during three years of study with implications for larval yellow perch growth and settlement. Currently, we have not included mortality and zooplankton fields (larval fish food) in our model. Future efforts will focus on these areas. Yet another issue to resolve is the assumption that fish larvae are passive particles; larval fish swimming ability increases with size, and swimming competence along with other behavioral patterns that can influence their horizontal and vertical distributions but are not captured in our model. Despite these apparent shortcomings, our modeling approach is consistent with many recent observations in Lake Michigan.

The hydrodynamic dispersal of young yellow perch provides a mechanism for the genetic homogeneity of the Lake Michigan yellow perch population. Miller (2003) reported that collections from southern basin collection sites in Michigan, Wisconsin, and Indiana were homogenous and not much different from those from Lake Michigan's northern basin. They were distinct from populations from Green Bay and inland lakes. The distinctiveness relative to Green Bay is likely due to a spawning period that occurs approximately one month earlier in Green Bay, and due to limited water exchange between Green Bay and Lake Michigan.

The timing for yellow perch to become demersal may be delayed for yellow perch in Lake Michigan. Whiteside et al. (1985) found that yellow perch from Lake Itasca, Minnesota, became demersal at about 25 mm total length. A similar length, 30 mm, was reported for Lake St George, Ontario (Post and McQueen 1988) and Lake Erie (Wu and Culver 1992). In contrast, trawling and seining records for Michigan (D. Jude, University of Michigan, Pers. Comm.), Illinois (J. Dettmers, Illinois Natural History Survey, Pers. Comm.), and Wisconsin (P. Hirethota, Wisconsin Department of Natural Resources, Pers. Comm.) indicate that demersal yellow perch smaller than about 40 mm are rare and most fish are 50 mm or more. Moreover, preliminary pelagic trawling has collected yellow perch from about 20 to 35 mm in late July and as large as 70 mm in mid-September. More detailed sampling and estimates of larval age and growth obtained from otolith increment analysis will be needed to determine how long perch remain pelagic in Lake Michigan. Assuming that the pelagic stage of perch is extended, it remains to be determined whether this will result in increased mortality.

It appears that the hydrodynamic conditions may produce a "source and sink" recruitment dynamic. The rocky habitat, preferred for spawning (Dorr 1982, Robillard and Marsden 2001) and presumably for feeding (Wells 1977, 1980, Janssen et al. in press, Janssen and Luebke in press) is primarily on the western side of Lake Michigan, and is perhaps most extensive in Illinois (Powers and Robertson 1968, Fucciolo 1993, Janssen et al. in press). The present modeling effort suggests that larvae originating from this preferred habitat would be mostly transported to the sandier and generally unconsolidated substrate along the eastern side of Lake Michigan. Much of the habitat along eastern Lake Michigan is now depauperate of potential forage for newly settled juvenile perch (Nalepa et al. 1998), which may impact survival in later life stages.

Our modeling effort represents a first step in integrating lake physics for understanding fish recruitment in the Great Lakes. Moreover, the modeling exercises presented here have shed light on how lake physics may modify and impact larval fish growth and survival in Lake Michigan. In addition, it has also exposed new questions in understanding the behavior (as driven movement) and ecology (size at which fish go demersal) of larval yellow perch, which may differ from other inland lakes.

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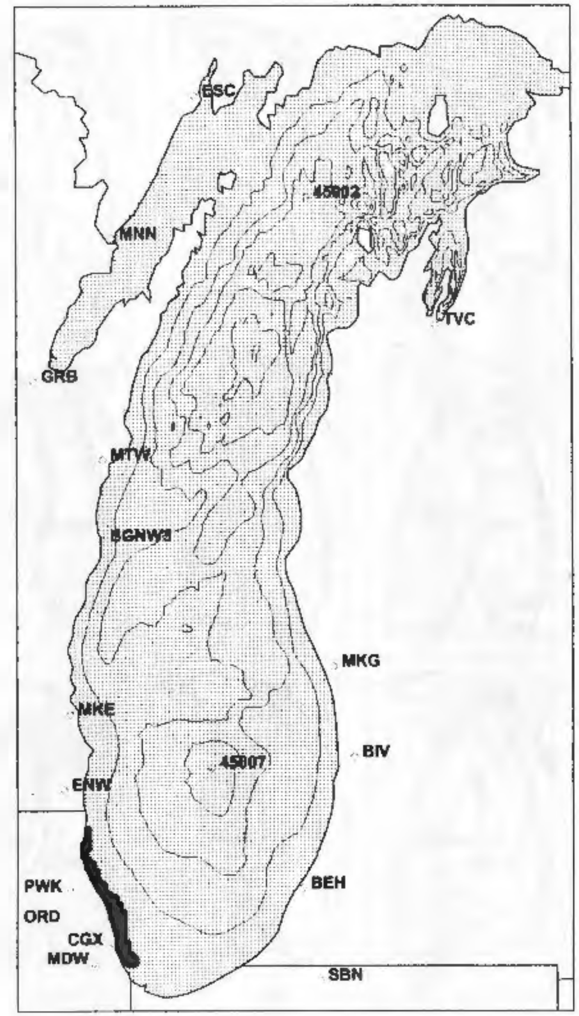

Figure 1. Numerical grid, bathymetry (isobaths every 50 m), and meteorological stations. Initial particles location in southern Lake Michigan is also shown.

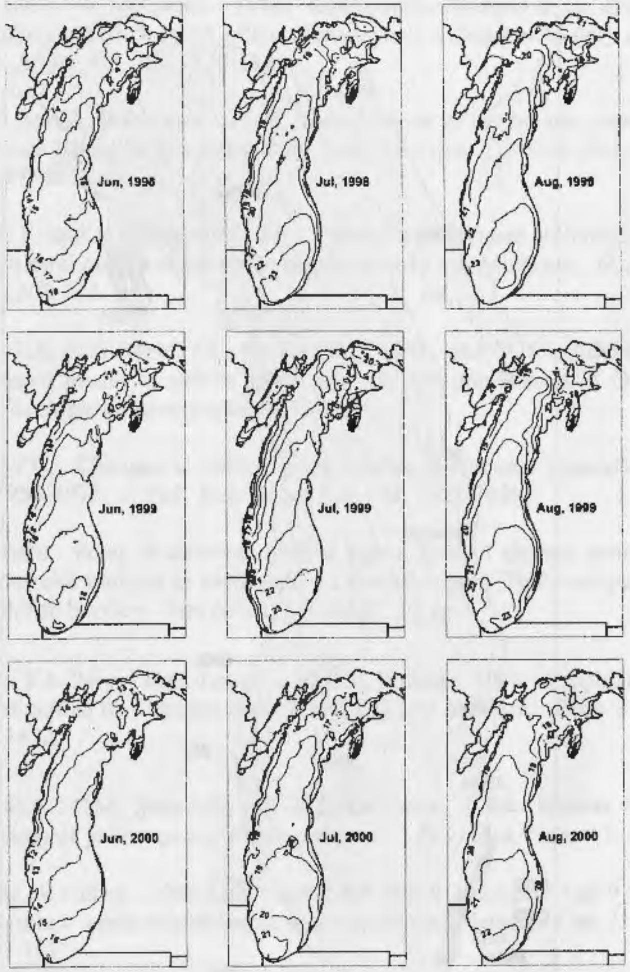

Figure 2. Lake surface temperature in 1998-2000

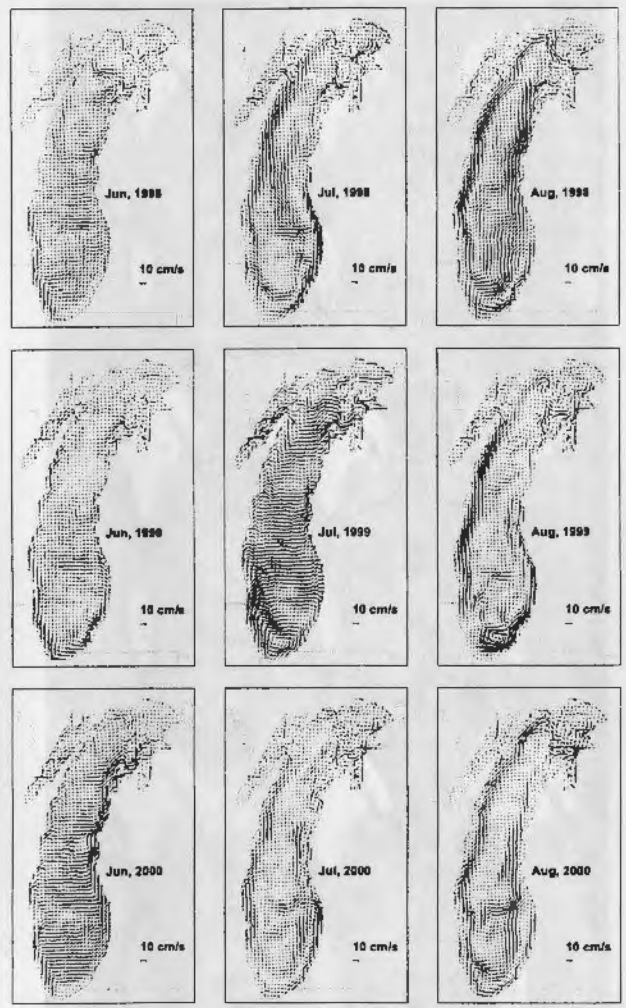

Figure 3. Surface currents in 1998-2000

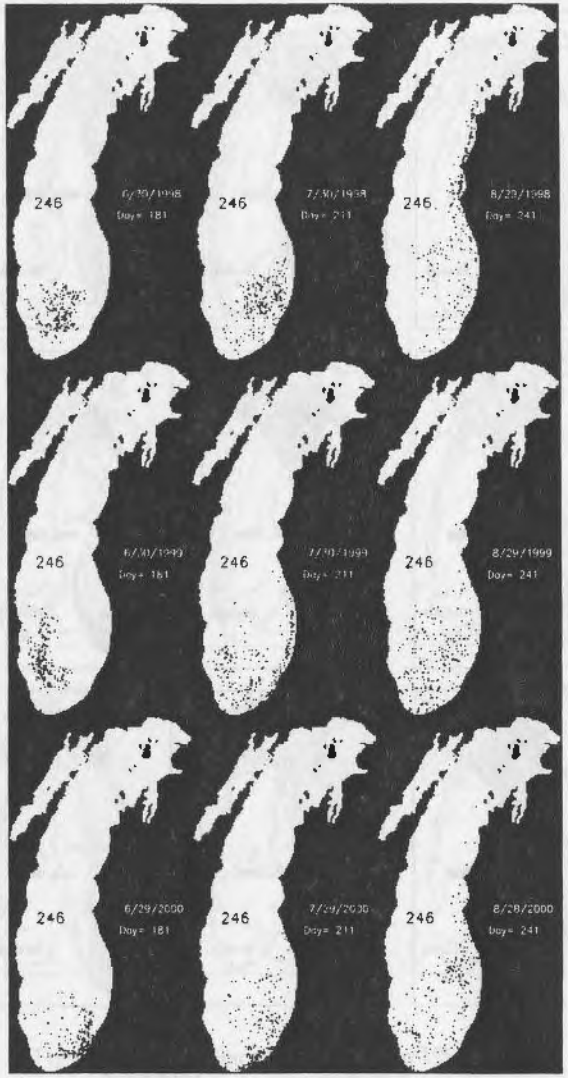

Figure 4. Particle transport in 1998-2000, total number of particles shown.

Figure 5. Larval transport and growth, Scenario 1 (see explanation in text). Total number of larvae reached 30 mm also shown.

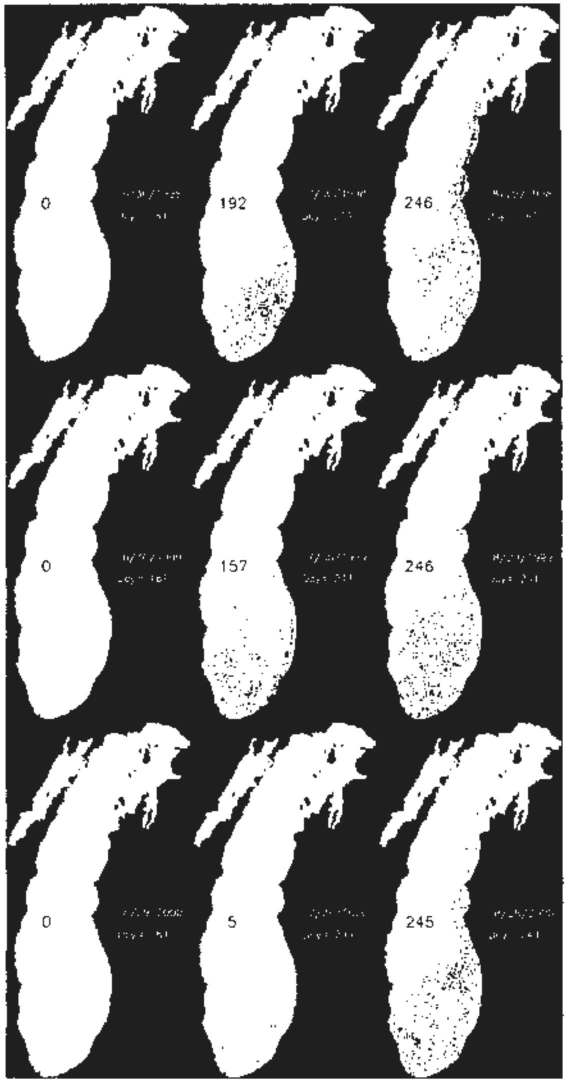

Figure 6. Larval transport and growth, Scenario 2 (see explanation in text). Total number of larvae reached 30 mm also shown.